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Is the length of the drying period critical for photosynthesis reactivation in lichen and moss components of biological soil crusts?

Silvana Munzi[a,*], Zulema Varela[a,b], Luca Paoli[c,d]

[a] cE3c, Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, 1749-016, Lisbon, Portugal
[b] Ecology Unit, Dept. Functional Biology, Universidade de Santiago de Compostela, Fac. Bioloxía, Lope Gómez de Marzoa s/n, Santiago de Compostela, 15702, A Coruña, Spain
[c] Department of Biology, University of Pisa, Via Luca Ghini, 13, 56126, Pisa, Italy
[d] CIRSEC, Center for Climatic Change Impact, University of Pisa, Via del Borghetto 80, 56124, Pisa, Italy

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ABSTRACT

Lichens and mosses represent the macroscopic components of biological soil crusts (biocrusts). Their ability to exploit short periods of water availability and reversibly deactivate metabolism is crucial for their growth and survival. In this work we investigated photosynthesis reactivation, respectively after long (65–66 days) and short (15 days) dry periods, in lichen and moss species widespread in two Mediterranean environments (Portugal and Italy). Chlorophyll *a* fluorescence emission of the samples was investigated and the parameter Fv/Fm, an indicator of vitality of photosynthetic organisms, was used as a proxy for photosynthesis reactivation. The fruticose lichens *Cladonia convoluta* and *C. rangiformis*, and the moss *Pleurochaete squarrosa*, typical of Mediterranean environments, showed a significantly slower reactivation of photosynthetic activity when subjected to a longer period of drought. Conversely, the alien invasive moss *Campylopus introflexus* was not affected by prolonged dry conditions. The study showed that drought duration influences the reactivation of photosynthetic activity in terricolous lichens and mosses forming biocrusts in re-hydration cycles. These results indicate the likelihood of a reduction in biocrust productivity as a consequence of climate change in Mediterranean drylands.

1. Introduction

The importance of biological soil crusts (biocrusts) has been widely recognized during recent years as we begin to understand the many ecosystem services that they provide (Maestre et al., 2011). In drylands, especially in Mediterranean ecosystems where desertification and soil erosion pose major environmental threats, biocrusts are particularly relevant for soil protection and soil-water-atmosphere dynamics (e.g. Morillas et al., 2016).

Lichens and mosses represent the macroscopic components of biocrusts (Belnap et al., 2016). The water content of these poikilohydric organisms, unable to avoid desiccation, depends directly on the environmental availability of water. Consequently, lichens and mosses spend their lives switching between hydrated and desiccated status (Green et al., 2011; Koster et al., 2010; Kranner et al., 2003 and references therein). The ability to reversibly deactivate their metabolism and exploit short periods of water availability is key to their growth and survival.

Desiccation tolerance is a common trait in organisms forming biocrusts, due to the extreme environmental conditions that characterize the soil surface, like frequent desiccation–hydration cycles and differences of temperature of about 15 °C within the first 5 cm of the soil surface (Kershaw, 1985). Desiccation tolerance is provided through cellular protection from desiccation-induced damage and cellular recovery and repair during rehydration (Kranner, 2002; Gao et al., 2017). Those adaptations can be constitutive or induced. In general, constitutive mechanisms act in the case of fast drying, while induced mechanisms are responsible in the case of acclimation (Kranner et al., 2008). Unsurprisingly, desiccation-tolerant species like lichens and mosses, that are frequently subjected to desiccation/hydration cycles (Green et al., 2011; Kranner et al., 2003 and references therein), mainly rely on constitutive mechanisms (Kranner et al., 2008). However, slow desiccation (happening in hours rather than minutes as in fast desiccation) is more favorable to recovery than fast desiccation and allows most lichens to remain viable in extreme conditions such as a water content of 5% or less and survive for long time at low relative humidity

* Corresponding author. Centre for Ecology, Evolution and Environmental Changes Faculdade de Ciências da Universidade de Lisboa, Campo Grande, Bloco C2, 6° Piso, sala 2.6.13, 1749-016, Lisbon, Portugal.
E-mail address: ssmunzi@fc.ul.pt (S. Munzi).

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(Kranner et al., 2008). One example of the inducible mechanisms is the rearrangement of protein complexes that is considered responsible for protecting lichens against irreversible photoinhibition during the desiccation period (Chakir and Jensen, 1999). Photoinhibition may be induced when absorption of light energy by photosynthetic pigments exceeds the rate of its consumption in chloroplasts and involves an inactivation of the primary photochemistry of Photosystem II (PSII) (Manrique et al., 1993). Similarly, in mosses, slow drying increases desiccation tolerance in many species, likely enabling protective mechanisms such as sugar and protein synthesis to be initiated (Proctor et al., 2007 and references therein).

Predictions for 2100 suggest that climate change will cause an increase in air temperature and a decrease in precipitation in the Mediterranean Basin region (Christensen et al., 2007), exposing Mediterranean ecosystems to longer and more abrupt periods of high temperatures and drought. It is therefore crucial for environmental protection and management to investigate how the biocrusts of Mediterranean drylands will respond to climate change, including longer periods of drought.

Desiccation time, rate of water loss, photoinhibition and relative water content are known as important factors controlling the impact of desiccation on desiccation-tolerant species, including lichens, mosses and cyanobacteria (e.g. Bar-Eyal et al., 2015; Belnap et al., 2016; Fukuda et al., 2008; Raanan et al., 2016). However, while the consequences of changes in warming and watering are largely considered by researchers around the world (e.g. Lafuente et al., 2018 and references therein), the effects of drought length on biocrusts have so far been investigated in few studies (e.g. Candotto Carniel et al., 2015; Harel et al., 2004; Kranner et al., 2003; Proctor et al., 2007).

In this work we investigated how the photosynthesis reactivation in terricolous lichens and mosses, responds to droughts of different length. Specifically, we compared the reactivation time in naturally dry samples. Our working hypotheses were that: (i) prolonged drought periods negatively affect the reactivation of photosynthesis in terricolous lichens and mosses in a Mediterranean environment, and (ii) invasive moss species are less sensitive than native species to differences in drought duration.

2. Materials and methods

2.1. Experimental design

The experiment was designed to compare the photosynthetic reactivation in common lichen and moss species following two dry periods of different extent in Mediterranean environments.

The fruticose (shrub-like), terricolous lichens *Cladonia convoluta* and *C. rangiformis* and the mosses *Pleurochaete squarrosa* and *Campilopus introflexus* were selected for the experiment. All of them are common species widely distributed in the Mediterranean basin. However, *C. introflexus*, a widespread moss in the Southern hemisphere, was only recently introduced into Europe (Sérgio et al., 2018) and its presence has been associated with environmental disturbance. It is considered one of the 100 worst alien species in Europe (Delivering Alien Invasive Species Inventories for Europe, http://www.europealiens.org/).

Lichens and mosses were collected in two sites far from pollution sources and with similar climatic conditions (Table 1): a Mediterranean cork-oak forest at Companhia das Lezírias, Samora Correa (Portugal) and in an open stand within a mixed oak forest in Miniere di Murlo, Siena (Italy). In both sites, lichen and moss samples were collected in their naturally dry state in spring and summer, after periods of around two weeks (short dry period) or two months (long dry period) without rain, respectively. Sampling occurred in Portugal on 30 July 2017, after 65 days without rain and on 22 May 2018, after 15 days without rain; and in Italy on 26 July 2017, after a dry period of 66 days and on 1 May 2018, after 15 days without rain. The individuals of these species were collected separately after the two different periods of drought, so they were not the same individuals.

Table 1
Characteristics of the sampling sites including average (on the last 30 years) ranges of temperature (T) and pluviosity (P), and microclimatic parameters during the experiment. L = lichen; M = moss. Meteorological data derived from the closest available monitoring stations (source: Meteoblue – Portugal; Settore Idrologico Regionale – Italy).

Parameters	Portugal	Italy
Site	Companhia das Lezírias	Miniere di Murlo
Type of environment	Mediterranean cork-oak forest	Mediterranean mixed oak forest
Coordinates (UTM WGS84, 32T)	519175 E; 4299714 N	693600 E; 4779010 N
T/P range in Winter	9-10 °C/200–300 mm	6-10 °C/70–200 mm
T/P range in Spring	12-14 °C/150–250 mm	13-20 °C/60–190 mm
T/P range in Summer	21-23 °C/20–40 mm	20-24 °C/40–70 mm
T/P range in Autumn	14-16 °C/150–250 mm	8-16 °C/100–250 mm
Selected species	*Cladonia convoluta, C. rangiformis* (L); *Campilopus introflexus* (M)	*Cladonia convoluta, C. rangiformis* (L); *Pleurochaete squarrosa* (M)
Short dry period	15 days	15 days
Precipitation	–	–
Temperature (average of max)	25 °C	23 °C
Long dry period	65 days	66 days
Precipitation	–	–
Temperature (average of max)	32 °C	32 °C

In each site, twenty independent samples of each species were collected at random within an area of about 50 m × 50 m, a minimum of 5 m from the nearest projected tree canopy. Samples were then transported to the laboratory where photosynthesis reactivation was measured.

Each day, dry samples (water content < 8% dry wt) were sprayed until completely moistened at 9:00, 14:00 and 18:00. Fluorescence measurements were taken every morning after the first hydration. Prior to each measurement, hydrated samples were dark adapted for 10 min, then illuminated for 1 s with a saturating (3000 μmol m^{-2} s^{-1}) red-light pulse and fluorescence emission was recorded for 1 s. Measurements were carried out with a Plant Efficiency Analyzer (Handy PEA, Hansatech Ltd, Norfolk, UK). The condition of the samples, as inferred from fluorescence data, was expressed by the maximum of quantum yield of primary photochemistry – Fv/Fm (a reliable proxy of the intrinsic efficiency of PSII and hence of the vitality of the samples). The parameter Fv/Fm corresponds to the expression (Fm – F0)/Fm, where F0 and Fm are minimum and maximum chlorophyll *a* fluorescence emission and Fv = (Fm − F0) is the variable fluorescence. Chlorophyll *a* fluorescence emission increases from F0, when all the reaction centres (RCs) of PSII are open, up to Fm, when all the RCs of PSII are closed. Optimal values for healthy lichens and mosses vary among 0.6 and 0.8, and samples of *X. parietina* were affected but still viable for Fv/Fm values > 0.32 (Munzi et al., 2013). The experiment was considered concluded when the Fv/Fm value reached a constant value, indicating the complete reactivation of the photosynthetic activity, and lasted one week in Italy (T0-T6 in Fig. 1) and six days in Portugal (T0-T5 in Fig. 1).

2.2. Statistics

Normality and homoscedasticity were checked with Kolmogórov-Smirnov and Levene tests, respectively. Data fit with the requirements of parametric statistical test, thus differences in recovery between long and short periods for each species were compared by one-way ANOVA using values of Fv/Fm as the dependent variable and the 2 different periods of drought as the independent variable. Significance levels were set at $P < 0.05$. All the tests were carried out using the package IBM SPSS Statistics version 24.0 (IBM, New York, NY, USA).

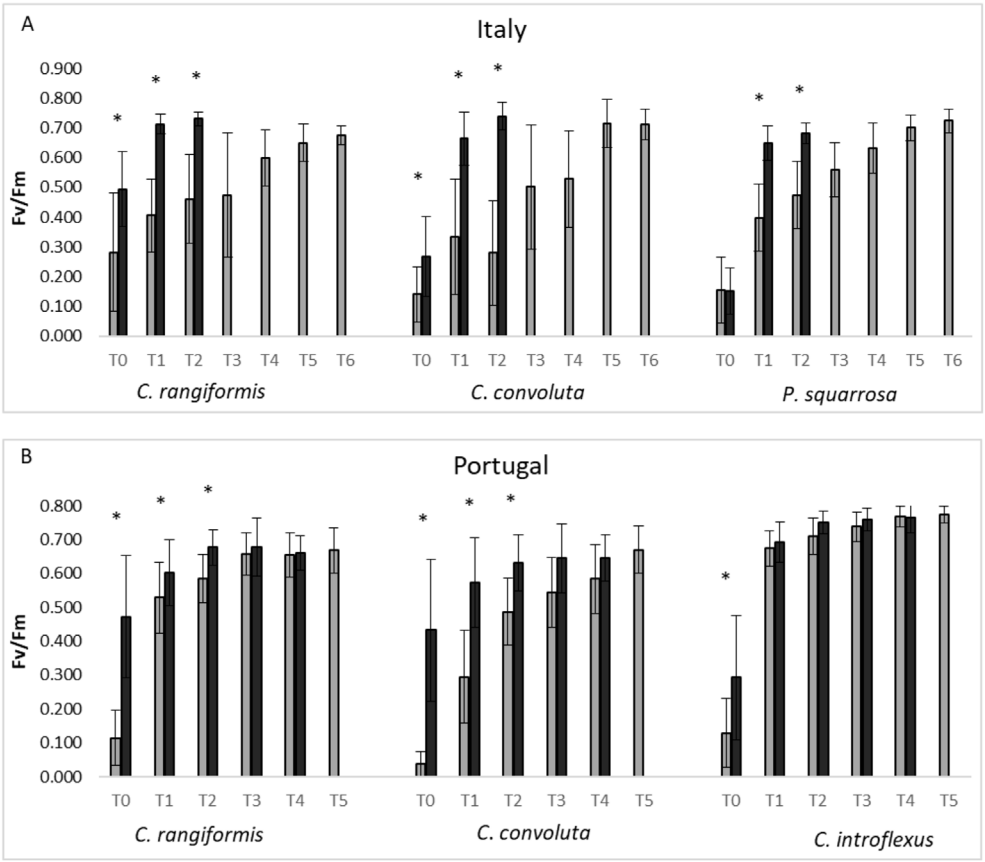

Fig. 1. Fv/Fm values (average ± SD; N = 20) for lichen and moss species in Italy (A) and Portugal (B). For each time (T), bars on the left (light grey) represent the long dry period and bars on the right (dark grey) the short dry period. * = Significant differences between periods ($P < 0.05$).

3. Results and discussion

The results of the experiment confirmed both working hypotheses. The desiccation-tolerant lichens *Cladonia convoluta* and *C. rangiformis* and the moss *Pleurochaete squarrosa* from Mediterranean environments showed a significantly slower reactivation of photosynthetic activity when subjected to a longer period of drought. Conversely, the alien invasive moss *Campilopus introflexus* was not affected by prolonged dry conditions (Fig. 1). *Pleurochaete squarrosa*, the most common moss in the Mediterranean area, was the only species with no differences at T0, but reactivation was faster after the short period.

A reduction in the content of photosynthetic pigments and the shutdown of the photosynthetic process are reversible responses commonly induced by dry conditions in biocrusts (Bar-Eyal et al., 2015). In dehydrated lichens, the photosynthetic activity shuts down and the absorbed energy is dissipated without damaging the photosynthetic apparatus (Kranner et al., 2008). Consequently, photosynthesis can be reactivated within "time-lags" ranging from a few minutes, if lichens are rehydrated with water, up to a few hours when lichens are rehydrated with high atmospheric humidity (Lidén et al., 2010).

Similar mechanisms occur in bryophytes, in which desiccation tolerance is a common phenotype and more than 200 mosses have been experimentally verified to be desiccation-tolerant (Gao et al., 2017).

Nevertheless, observations made on desiccation-tolerant, biocrust-forming organisms, showed that drought duration can influence the reactivation of photosynthetic activity during re-hydration cycles. For example, Kranner et al. (2003) found that prolonged storage of lichen thalli in the desiccated state can lead to a reduction of chlorophyll *a*: 45% in *Lobaria pulmonaria* and 40% in *Peltigera polydactyla* after 9 weeks in a desiccated state. Analogously, in the moss *Anomodon viticulosus*, after six to seven weeks desiccation, re-hydration caused a metabolic disruption from which the moss could barely recover. In that case, the repair was less efficient, and regeneration and regrowth of the moss relied on functional isolated cells or patches of tissue (Proctor et al., 2007).

Harel et al. (2004) found that soil cyanobacteria from desert biocrusts exposed to almost daily rehydration/desiccation cycles could reactivate PSII within a few minutes. However, samples maintained in the dry state for longer periods, e.g. 6 months, needed at least 60 min or more than one rehydration/desiccation cycle to activate PSII. Similarly, Proctor et al. (2007) found that in bryophytes the time required to recover from desiccation increased and the degree of recovery decreased with the length of desiccation. Samples desiccated for more than 15 days exhibited a progressively slower and less complete recovery when compared with those desiccated for only a few days. Finally, Candotto Carniel at al. (2015) investigated the effects of desiccation on the lichen *Parmotrema perlatum* and on its isolated, cultured photobiont *Trebouxia* and found that extending the exposure period at 3% RH caused an increasing photoinhibition over time in both re-hydrated lichenized and non-lichenized algae.

Our findings confirmed that, in organisms subjected to different drought lengths, photosynthesis reactivation takes different times. This suggests that prolonged dry conditions in lichens and mosses cause progressive damage that can be repaired but only when they have sufficient time in the hydrated status. In addition, species-specific characteristics and differences in growth conditions may also affect the rate of recovery after rehydration (Harel et al., 2004).

As observed in plant seeds, desiccation-tolerant organisms can undergo the process of vitrification where a high concentration of sugars in the cytoplasm leads to the formation of intracellular "glasses", characterized by high viscosity. In this condition, molecular mobility decreases, and deleterious chemical reactions are slowed down (Proctor

et al., 2007; Candotto Carniel et al., 2015). However, processes such as lipid peroxidation (the oxidative degradation of lipids), de-esterifications (rupture of molecular bonds) and other potentially harmful reactions can still take place and reduce viability over long periods (Candotto Carniel et al., 2015).

Temperature is another factor potentially contributing to the observed results. In our experiment, both the dry periods started in Spring, but samples collected in July were subjected to higher temperature than the ones collected in May. Temperature affects processes such as dehydration speed of poikilohydric organisms. In turn, slow desiccation is responsible for longer viability of lichens at low water content and for a better recovery of mosses after rehydration (Kranner et al., 2008; Proctor et al., 2007 and references therein).

High temperatures can reduce the residual amount of water in desiccated tissues. Fernández-Marín et al. (2013) demonstrated that in the moss *Syntrichia ruralis*, enzymatic activity was still detectable even at very low water content. Since desiccation tolerance is mainly provided by cellular processes, even small quantities of water can be important to permit minimal metabolic activity and maintain protection mechanisms against desiccation. Accordingly, Chakir and Jensen (1999) found that inactivation of photosynthesis during drying and osmotic stress in *Peltigera aphthosa* and *L. pulmonaria* responded differently to a mild or a severe stress, depending on lichen water potential.

These findings suggest that the relationship between temperature, length of drought and photosynthesis reactivation must be further explored to identify the most important stressors and the synergies affecting biocrust performance and recovery. This will contribute to model global change scenarios more precisely and will give important indications for the implementation of conservation/restoration programs.

Noteworthy, the response of *C. introflexus* was different from the other species since it was not affected by the duration of drought. *Campilopus introflexus* is an alien invasive moss spreading across Europe thanks to its high ecological tolerance (Hugonnot, 2017). It is reasonable to hypothesize that the capacity to recover from desiccation more quickly than other moss species, as observed in our study, favours its invasion into environments with limited water availability.

According to future climate change scenarios, the ecological consequence of increasing duration of dry periods will lead to reduced productivity of biocrusts, with the consequent reduction in the ecosystem services they provide. Extended droughts will mean longer periods of inactivity of poikilohydric organisms, and also slower resumption of photosynthetic activity. In sensitive ecosystems like drylands, where biomass production in slow-growing communities is restricted, a net cumulative loss of carbon over repeated cycles of dehydration/rehydration could lead to an impairment of ecosystem functioning. In addition, in these conditions, shifts in community composition and biodiversity loss can also be hypothesized, where more tolerant and fast-growing species, e.g. invasive species, will replace sensitive ones.

4. Conclusions

This study showed that drought duration, likely in combination with high temperatures, affects the capacity of photosynthetic reactivation in terricolous lichens and mosses belonging to biological soil crusts.

The predicted increase in air temperature and the decrease in rain events in Mediterranean environments will therefore have important consequences: a net cumulative loss of carbon over repeated cycles of dehydration/rehydration; increased likelihood of invasion by species with a more efficient recovery rate leading to a loss of biodiversity.

The relationship between temperature, drought duration and photosynthesis reactivation in protective biocrusts must be further explored to maximize their protective role in drylands, threatened by desertification and soil erosion.

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